

REPRODUCTION AND SURVIVAL OF THE PILEWORM *NEREIS SUCCINEA* IN HIGHER SALTON SEA SALINITIES

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The Salton Sea is a large (200 square miles) closed salt lake in a below-sealevel depression in the Colorado Desert of southeastern California. The Sea was formed accidentally from 1905 to 1907 when flood waters of the Colorado River broke through poorly constructed headgates of an irrigation canal. Following repair of the break, the new Salton Sea evaporated to a low of 250 feet below sea level by 1925. Since then the Sea has gradually increased in volume and surface elevation because agricultural waste water inputs exceed the annual evaporation of about 6 feet. In 1977, surface elevation was -228 feet, highest since 1914, and salinities averaged about 37‰ in summer. Early history of the Salton Sea is given by MacDougal (1914), and later history by Walker (1961).

The original biota of the Salton Sea, freshwater organisms from the Colorado River and a few species native to desert springs, died out by the mid-1920's. Attempts to introduce sportfishes did not succeed until the early 1950's, with the establishment of the croaker (*Bairdiella icistia*), sargo (*Anisotremus davidsoni*), and orange-mouth corvina (*Cynoscion xanthulus*), all from the Gulf of California. Several successful introductions of invertebrates have also occurred. The Salton Sea is eutrophic and highly productive (Walker, 1961), but as there are no planktivorous fishes, most plankton die and are converted to benthic detritus (Arnal, 1961). *Nereis* (*Neanthes*) *succinea* Leuckart, a polychaete annelid introduced in 1930, is the most important benthic detritivore and the most important food source for the sportfishes. The quasi-marine ecosystem of the Salton Sea is discussed by Walker (1961) and Young (1970). Ecology and reproductive biology of *N. succinea* in the Salton Sea have been discussed by Carpelan and Linsley (1961a, b) and Walker (1961).

With the salinity of the Salton Sea approaching 40‰ in the early 1970's, much concern has been expressed over the future of the sportfishery, one of the most important in California (Hanson, 1972). Increasing development of local geothermal energy resources may result in spills of highly saline waste brines into the Sea, which may also affect the sportfishes or their food supply (Shinn, 1976). Reproduction by the three sportfishes is limited to salinities below 40‰ (Brocksen and Cole, 1972; Lasker, Tenaza, and Chamberlain, 1972; May, 1975, 1976). There is little published information on high salinity adaptations in polychaetes (Bayly, 1972; Oglesby, 1978), and only one published study on the effects of higher salinities on *N. succinea* in the Salton Sea. Hanson (1972) observed that pileworms survived 96-hr exposures to salinities as high as 67.5‰, but speculated

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that "reproduction of the pileworm would probably be adversely affected at lower salinities."

It is the purpose of the present study to establish upper salinity limits for reproduction and survival of *N. succinea* in Salton Sea waters, in order to assess the possibility that pileworm failure due to increased salinity from either evaporation or brine spills may adversely affect the sportfishery.

MATERIALS AND METHODS

Pileworms were collected from the northeastern Salton Sea, at Mecca Beach in the Salton Sea State Recreational Area. Worms were picked by hand from shallow sediments, particularly from barnacle shell rubble cemented with gypsum crystals. While a few heteronereids could be collected from the benthos in this fashion, it was necessary to collect by night-lighting in order to secure adequate numbers for experiments on fertilization and development.

In the laboratory, worms were maintained in glass tubes in finger bowls, covered to reduce evaporation. For most experiments worms were maintained at 21 to 23° C; for some experiments, worms were kept at 34° C, somewhat warmer than summer water temperatures in 1976-77, but not as warm as maximum water temperatures of 36° C recorded by Walker (1961).

Salton Sea water was collected from Mecca Beach. Higher salinities were made by evaporating 36‰ Salton Sea water at about 50° C until it reached a concentration of about 90‰. This was then mixed with 36‰ Salton Sea water to provide a full range of salinities. During the concentration process, calcium salts precipitated. Thus, in the final mixtures, calcium may have been somewhat undersaturated. For some experiments media were made up from Instant Ocean, an artificial salt mixture resembling ocean sea water in ionic ratios. All media were routinely filtered through activated charcoal in Whatman Grade 3 filter paper before use. Media were changed in the culture dishes daily. No antibiotics were used.

Laboratory fertilizations were carried out according to the procedures detailed in Costello, Davidson, Eggers, Fox, and Henley (1957) and Smith (1964). Water was changed daily, involving some loss of developmental stages by decanting. In some cultures, bacterial or protozoan contamination was present; however, this did not pose a severe problem experimentally. Since no supplemental food was supplied to the developing larvae, cultures died at a late trochophore or early 3-setiger stage.

Salinities in the field and during ordinary laboratory operations were measured with an American Optical total solids refractometer, calibrated against known solutions measured with a Hewlett-Packard vapor pressure osmometer and with a Buchler-Cotlove chloridometer. Chlorinities were converted to ‰ Salton Sea water using the ion ratios given in Carpelan (1958), Walker (1961), and Young (1970).

RESULTS

Effects of higher Salton Sea salinities on survival of atokous worms

Experiments on survival of large atokes (immature worms) involved either direct transfers to the full range of salinities, or gradual increases of salinity in

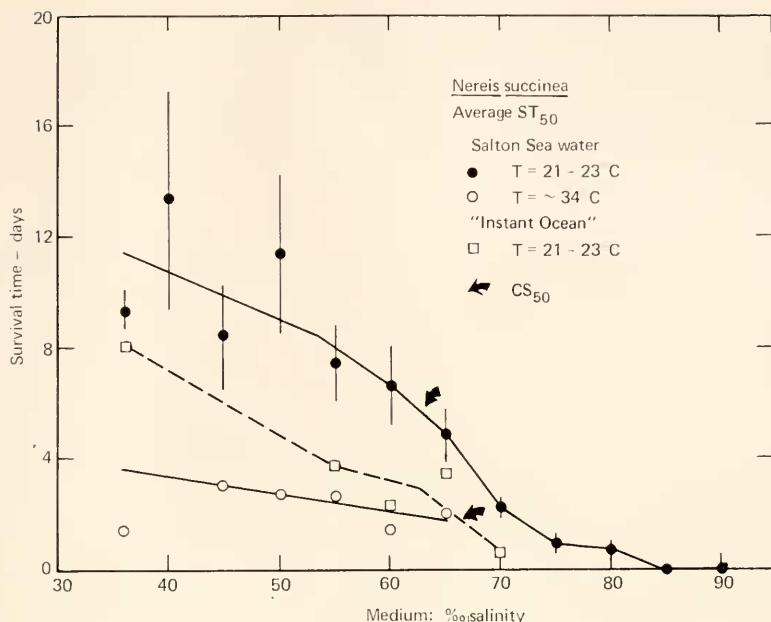


FIGURE 1. Survival time of *Nereis succinea* in increasing concentrations of Salton Sea water, expressed as average ST₅₀. Points are averages of all trays (initially 10 worms each) in each salinity, with the standard error indicated. Arrows indicate the Critical Salinity (CS₅₀) where survival is reduced to 50% of that in 36‰ Salton Sea water.

increments of 10‰ until the final test salinity was reached. Calculation of the time for 50% survival (ST₅₀) of a test group of worms (usually four trays with 10 worms each) began with the day the worms first were placed in the final test salinity. Graphs of ST₅₀ as a function of the final salinity were used to determine the Critical Salinity (CS₅₀), the salinity where survival is reduced to 50% of the survival in 36‰ Salton Sea water. This calculation of CS₅₀ is possibly biased in those experiments involving graduated salinity increases, since it ignores the mortality of worms in lower salinities during the adaptation period. However, otherwise comparable experiments in which worms were transferred directly to the final salinities gave similar results. Results of both types of experiments are combined for the following analyses.

Results for all experiments on survival of atokes are summarized in Figures 1 and 2. These are averages and calculations based on over 280 worms in 36‰, over 140 worms in each salinity between 45 and 60‰, and between 50 and 100 worms in all higher salinities. Figure 1 shows the average survival time (ST₅₀) for all worms in all salinities, with the standard error indicated. Survival was high at salinities of 50‰ and lower, but declined in higher salinities. The critical salinity CS₅₀ is estimated to be slightly lower than 65‰. Figure 1 also provides the results of two related experiments: the effects of elevated temperature (34° C rather than the usual 21–23° C), and the effects of transfer to Instant Ocean. In both cases, overall survival seems to be diminished as compared with worms in

Salton Sea water in 21 to 23° C, though the general pattern is similar. For worms in Instant Ocean, CS_{50} is estimated to be somewhat higher than 65‰. It was not possible to provide an estimate of CS_{50} for the worms at 34° C, for it was higher than the highest salinity used in this experiment, 65‰. It appears that the Critical Salinity is not lowered for Salton Sea pileworms exposed either to ocean sea water or to temperatures only slightly lower than maximum summer water temperatures in the Salton Sea.

Much of the variability in the estimates of average ST_{50} (Fig. 1) is caused by the fact that in all salinities, all the worms in a given tray often would die soon after the first worm died, presumably because of the accumulation of toxic materials before the medium was changed. Not only is variability increased by this phenomenon, which may not be salinity-related, but also the average ST_{50} is decreased. Die-off of entire trays of 10 worms was particularly a problem at 34° C, due to increased bacterial activity. In order to provide an estimate of survival that avoids this problem, Figure 2 shows the survival time for the longest surviving worm in each salinity. At least some pileworms survived longer than the length of the experiments in nearly all salinities of 65‰ and lower, over 4 weeks for the worms in Salton Sea water at 21 to 23° C, and over 2.5 weeks for the worms in Instant Ocean and in 34° C. At higher salinities maximum survival time declined rapidly. No worms survived even a day at salinities higher than 85‰ at 21 to 23° C, nor higher than 75‰ in Instant Ocean. In both these experiments, CS_{50} was 70‰. No salinities higher than 65‰ were used in the experiments at 34° C, and since at least one individual lived as long as 8 days in this salinity, it is not possible to estimate CS_{50} , which must be higher than 65‰.

Most worms in the laboratory did not survive more than a week or two, even when maintained in 36‰ Salton Sea water. Carpelan and Linsley (1961a) indicated that *N. succinea* takes over a month to reach sexual maturity in the Salton Sea, so presumably pileworms must live well over a month in their natural habitat waters. Diminished survival in the laboratory may be a consequence of accumulation of metabolites, to lack of adequate food, or to other artificial causes. For these reasons, the survival times of pileworms in these laboratory experiments should not be taken as an exact counterpart of survival in the Salton Sea as salinity there increases. Rather, these laboratory results should be taken as an index of survival.

Both indices of survival (Figs. 1, 2) indicate that atokous pileworms survive increased Salton Sea salinities up to 60 to 65‰. Survival is considerably diminished at salinities in excess of 70‰, with no survival above 85‰, a concentration which is well over twice the present concentration of the Salton Sea. Even high summer water temperatures of 34° C do not decrease the survival limits of the pileworms. There is no indication that pileworms live longer in ocean water than in Salton Sea water.

Effects of higher Salton Sea salinities on heteronereid development

Studies of sexual development and spawning indicate that while *N. succinea* breeds year-round in the Salton Sea, reproductive activity is somewhat depressed during the summer months of high water temperature (Carpelan and Linsley,

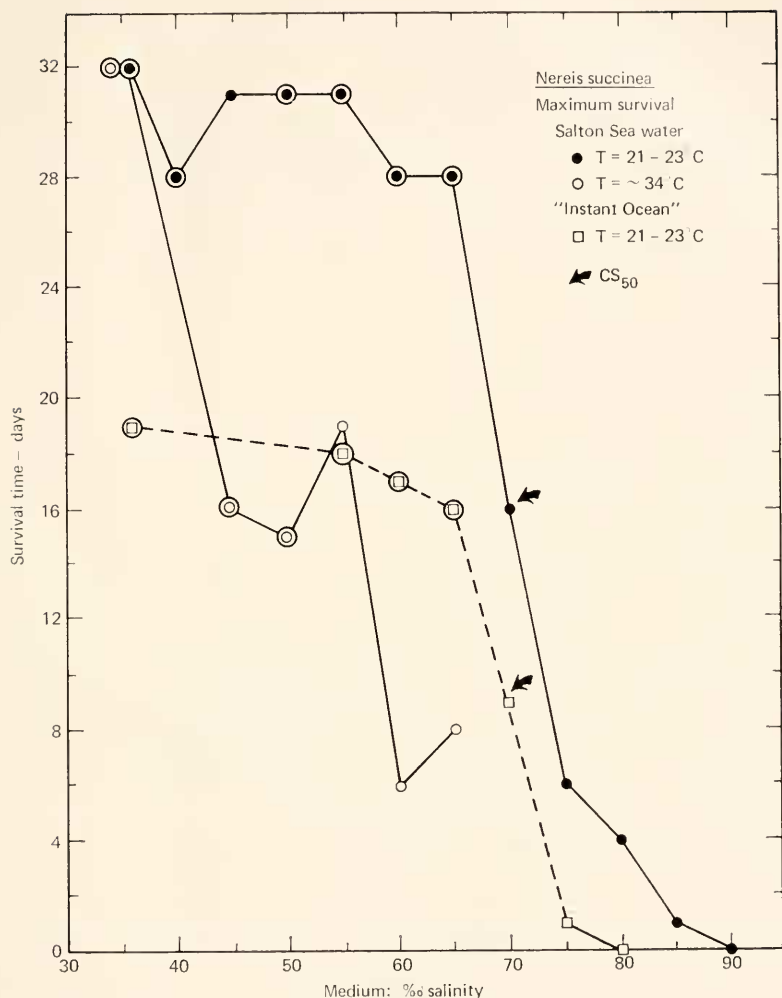


FIGURE 2. Maximum survival time of *Nereis succinea* in increasing concentrations of Salton Sea water. Circled points are those where worms were still alive by the end of the experiment.

1961a, b). Nevertheless, heteronereids (sexually mature adult worms) were collected throughout the summers of 1976 and 1977. The sex ratio of worms collected from the benthos at Mecca Beach was about one-third males and two-thirds females. As noted by Costello, *et al.* (1957) and Carpelan and Linsley (1961a), the sex ratio of swarming heteronereids is strongly reversed, males outnumbering females by about 10 to 1. This was also the case in our own collections. Heteronereids regularly developed in laboratory cultures, with the sex ratio comparable to that encountered in benthic worms during collection, about 2:1 females to males.

Heteronereid development in the laboratory was strongly influenced by salinity

(Fig. 3). About 15% of the pileworms maintained in low salinities (36 and 40‰) matured as heteronereids during the summer of 1977. A somewhat lower percentage (just under 12%) matured in 50‰, but in higher salinities maturation of heteronereids was greatly depressed, and there was no maturation in salinities of 70‰ or higher. There may be a differential effect of higher salinities on maturation of the two sexes, development of males being more strongly depressed than that of females. This observation may be an artifact of very small numbers of hetero-

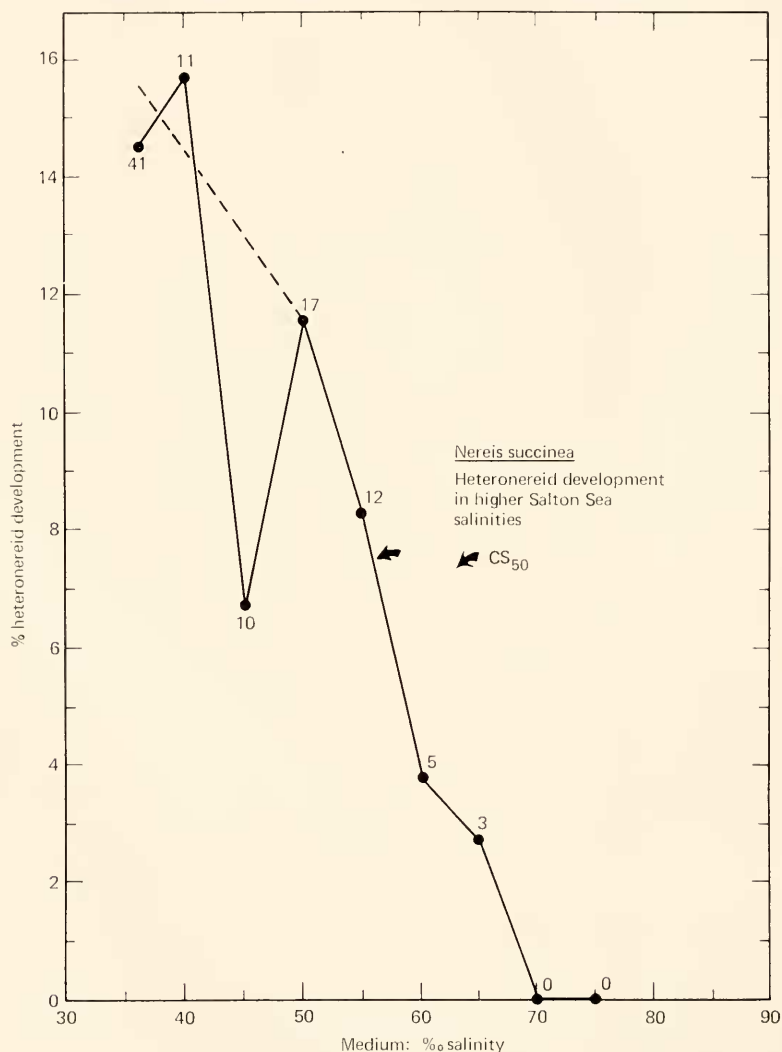


FIGURE 3. Effect of increasing Salton Sea salinities on heteronereid production by *Nereis succinea*. Actual numbers of heteronereids produced are indicated. Arrow indicates CS_{50} where heteronereid production is reduced to 50% of that in 36‰ Salton Sea water.

nerereids in the higher salinities. The estimated CS_{50} for heteronereid development is about 55‰ (Fig. 3).

Effects of higher Salton Sea salinities on fertilization and larval development

Laboratory fertilizations, using heteronereids either collected directly from the Salton Sea or produced in laboratory cultures, were readily accomplished. Development of larvae in 36‰ Salton Sea water appeared normal, and had the same time course as in previous studies on Salton Sea worms (Carpelan and Linsley, 1961a, b) and on this species at Woods Hole (Costello, *et al.*, 1957). In all these studies, temperatures were similar, about 20 to 25° C.

Fertilization in various salinities. Fertilization of eggs of *N. succinea* could be accomplished at salinities as high as 50‰, although the percentage of successful fertilizations was much reduced at 50‰. In one experiment, there was less than 5% successful fertilization at 55‰, and in a second experiment, no success at this salinity. In these experiments, eggs from females maintained in 36‰ were initially transferred to culture dishes containing 100 ml of the experimental salinity, and sperm from males opened in 36‰ added. Eggs transferred to salinities of 45‰ and higher shrank from osmotic water loss immediately after the transfer. Shrinkage was particularly noticeable in 50‰ and higher, many eggs becoming greatly distorted. It is estimated that the CS_{50} for fertilization is 45‰. While there was a small proportion of apparently successful fertilizations in 55‰ in one experiment, there was no further development even to the first cleavage. The highest salinity in which any development takes place following fertilization is 50‰. These results are summarized in Figure 4.

Fertilization in 36‰ Salton Sea water, followed by transfers to various salinities. Smith (1964) demonstrated that later developmental stages of *N. diversicolor* were less sensitive both to lower and to higher salinities than early stages. To determine if this is the case with *N. succinea*, several experiments were conducted in which eggs were fertilized in 36‰ Salton Sea water and embryos transferred to higher salinities at several different times during development.

In the first group of experiments, eggs were transferred as soon as possible after fertilization into a full range of salinities. There was excellent survival and subsequent development in salinities up through 45‰, although in 45‰ there was some evidence of shrinkage, and a few zygotes cleaved abnormally. These abnormally cleaving embryos (such as "dumbbells" which cleaved no further, and irregular cell clusters) did not develop successfully. There was poor survival of embryos transferred to 50‰, with abnormal cleavages and much shrinkage, but a few normal trochophores developed at this salinity. At 55 and 60‰ there was temporary survival, a high proportion of abnormal cleavage patterns, and no successful development. Embryos transferred to salinities higher than 60‰ shrank excessively and showed no type of cleavage. These early cleavage stages seem as sensitive to higher salinities as fertilization itself; it is estimated that the CS_{50} for early cleavage is 45‰, with no successful development higher than 50‰. These results are summarized in Figure 4.

This same experiment was conducted at 34° C to determine if summer water temperatures were more stressful on development than 21 to 23° C. There were

no observed differences in survival and developmental success between 34° C and 21 to 23° C, other than a considerable acceleration of cleavage at the higher temperature. There seems to be no additional stress on development in temperatures as high as summer water temperatures in the Salton Sea. On the other hand, in either temperature regime, development in salinities of 45‰ was markedly delayed as compared with development at lower salinities.

In a second group of experiments, fertilized eggs were allowed to develop in 36‰ Salton Sea water until the early trochophore stage, about 8 to 10 hr. These early trochophore stages were then transferred to salinities up to 75‰. There was excellent survival and development at all salinities up through 50‰. No shrinkage of trochophores was noticed at 45‰. In 50‰ there was some shrinkage, and trochophore cilia ceased beating temporarily. At 55‰ these shock effects were more severe, but there was considerable survival and subsequent development. At 60‰ there was no recovery of ciliary motion following transfer, and while it was estimated that perhaps 5% of the early trochophores survived the transfer, there was no subsequent development. There was no survival at higher salinities. Thus, early trochophores are less sensitive to high salinities than earlier cleavage stages. The estimated CS_{50} is 50‰, but there was no development above 55‰. These results are summarized in Figure 4.

In the final experiment, fertilized eggs were allowed to develop in 36‰ Salton Sea water until the swimming trochophore stage, about 24 hr. Swimming trochophores were then transferred to salinities up to 75‰, and survival and subsequent development monitored to the beginning of segmentation about 18 hr later. Survival was not as good as in the experiments involving transfers at earlier stages, but there was some survival and development up through 55‰. Swimming trochophores transferred to 50 and 55‰ showed some shrinkage, and ciliary activity temporarily stopped. In 60‰ these shock effects were more severe, and survival was low; however, some trochophores were still alive after 18 hours, though development had not progressed. In higher salinities there was little or no survival following transfer, shock effects were very severe, and there was no subsequent development. It appears that swimming trochophores have about the same sensitivity to higher Salton Sea salinities as do early trochophores. These results are summarized in Figure 4.

DISCUSSION

The present experiments supplement and extend the results to Hanson (1972) in showing that atokous *N. succinea* can survive for extended periods of time in very high Salton Sea salinities, at least as high as 65‰, with perhaps some reduction of survival in 70‰. There is short term survival in salinities as high as 80‰, more than twice the present salinity of the Salton Sea. There are reports of nereid and other polychaetes in high salinities in lagoons and estuaries, but few reports are for salinities in excess of 50‰ (Bayly, 1972; Oglesby, 1978). There have been no experiments on any of these other polychaetes to determine actual upper salinity tolerances, or if they actually breed in such high salinities.

Hanson's (1972) prediction that reproduction of the pileworm in the Salton Sea would be adversely affected at salinities lower than the limit for adult sur-

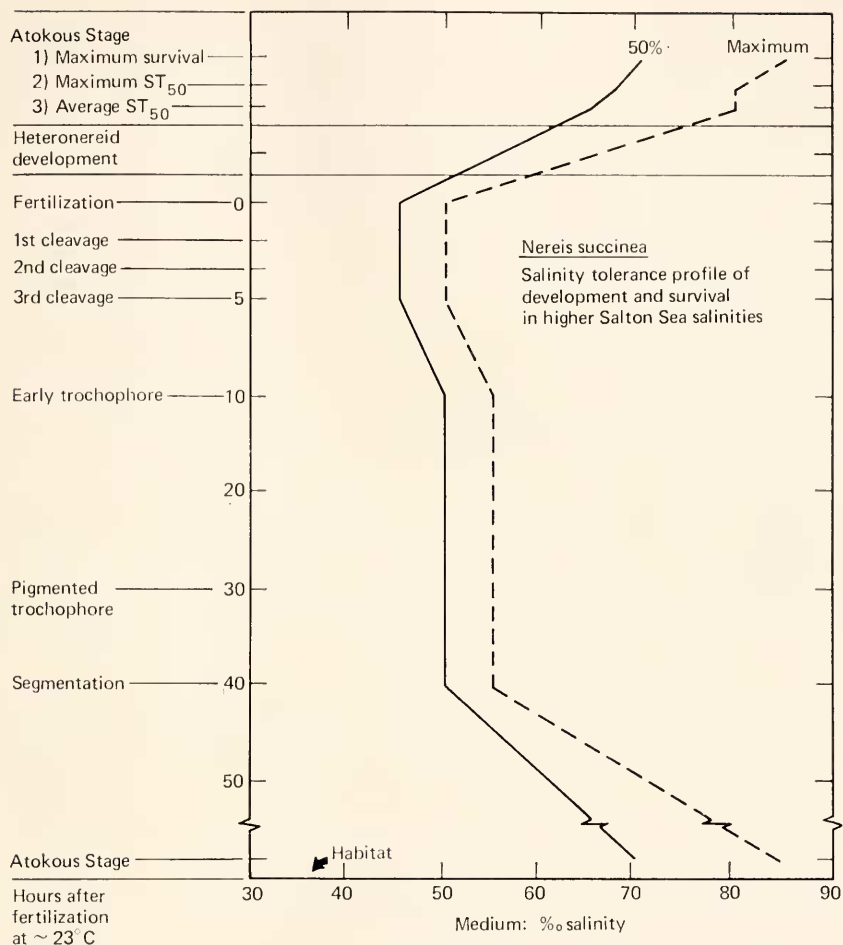


FIGURE 4. Salinity tolerance profile of development and survival of *N. succinea* in higher Salton Sea salinities. Stages and times are approximate for 21 to 23° C. The solid line indicates the Critical Salinity (CS₅₀), where survival and development are reduced to 50% of that in 36‰ Salton Sea water. The dashed line indicates the maximum salinity at which any survival or development occurred.

vival is confirmed by these experiments, for there was no successful fertilization or cleavage in salinities higher than 50‰, and reasonable success was limited to salinities of 45‰ and lower. Early and late trochophores could tolerate somewhat higher salinities, up to 50‰. Assumption of the high salinity tolerance of the atokes must come later in development than the appearance of segmentation, the termination of the present experiments.

Table I summarizes the literature on the effects of low salinities on development of *N. succinea*. Taken together, these reports suggest that *N. succinea*, like many other estuarine and marine polychaetes, cannot reproduce at salinities below the horohalimum of 5 to 8‰ (Oglesby, 1978), even though atokous *N. succinea* can

survive at considerably lower salinities (Oglesby, 1965; Hogue and Oglesby, unpublished results). The report by Foster (1972) that *N. succinea* can survive in fresh water is not supported by published data (Oglesby, 1965, 1978). The studies summarized in Table I, combined with the present results, provide a picture that is comparable to *N. diversicolor* (Smith, 1964), showing a "bottleneck" of salinities above and below which cleavage is blocked (Fig. 4). That is, while adult and atoke survival limits range from about 1‰ to as high as 80‰, development is successful only between 10 and 45‰.

It is premature to conclude that when the Salton Sea finally exceeds 45 to 50‰, reproduction of *N. succinea* will be blocked. As Smith (1964, 1977) has discussed, at least some of the reason for lack of reproductive success at extreme salinities may be mechanical, due to osmotic swelling in low salinities and osmotic shrinkage in high salinities. Shrinkage was very apparent in the present experiments at 50‰ and higher in eggs and embryos transferred from 36‰. It would have been desirable to attempt fertilizations with eggs and sperm taken from adults adapted to much higher salinities, to avoid the initial osmotic problem. However, even though heteronereids were produced in the laboratory in salinities as high as 65‰ (Fig. 3), never were a male and a female mature at the same time in a salinity higher than 36‰. Smith (1964) reported that some populations of *N. diversicolor* in northern Europe reproduce in salinities greater than the upper salinity limit for reproduction of other populations of the same species. It may

TABLE I
*Effects of lower salinities on development of Nereis succinea**

Stage and treatment	Observed effects on development	Reference
Unfertilized eggs	Survival down to 9.6‰.	Just (1928)
Fertilized eggs	Very low resistance to dilute sea water.	Just (1928)
Development in 91‰ SW after 1 hr exposure to dilute SW	Normal development above 16‰; diminished success at 11–14‰, though some eggs develop normally.	Just (1930a)
Development in varied SW after fertilization in 91‰ SW	Normal development above 16‰; diminished success at 14‰, but some normal development; cleavage but not trochophores in 11, 13‰.	Just (1930b)
Development in varied SW after fertilization in 100‰ SW	Normal development of nectochaeta larva in 14–35‰; normal development of trochophore in 8‰; no cleavage in 2–6‰.	Kinne (1954)
Development in varied SW and temperatures after fertilization at 20‰	Development at 10, 15, 20‰, except none at 10‰ at 10° C. Development accelerated at higher salinity and higher temperature.	Dean and Mazurkiewicz (1975)

**Nereis limbata* Ehlers, the name used by Just (1928, 1930a, b) is synonymous with *N. succinea* Leuckart. Just (1928, 1930a, b) did not provide the actual concentration of his "100‰ SW." Salinities presented in this table are based on data of Cole (1940) for summer water salinities at Woods Hole. Since there are no significant fresh-water inflows in the area, it is reasonable to assume that Woods Hole summer sea water averages about 32‰, or 91% of 35‰ salinity.

be that as the salinity of the Salton Sea gradually rises, there will be genetic selection for *N. succinea* with higher limits for reproductive success.

Developmental events were somewhat slowed at higher salinities, but at salinities below 45 to 50‰ development was otherwise normal. Smith (1964) observed that low salinities also delayed development, particularly cleavage, in *N. diversicolor*.

The present experiments indicate that temperatures as high as 34° C do not have any marked effect on adult survival and reproduction in *N. succinea*. At the present time there is year-round reproduction in the Salton Sea, and this pattern should continue as long as the overall salinity itself does not become too high.

Interestingly, Salton Sea pileworms do not seem to have reduced survival in Salton Sea water as compared with ocean water (Figs. 1, 2). May (1976) found that eggs and larvae of the croaker *Bairdiella* survived well in sea water, but had very poor survival in Salton Sea water of the same salinity. He suggested that this poor survival of the fish was related to the unusual ionic composition of the Salton Sea. This seems not to be a problem with *N. succinea*.

Spills of geothermal waste brines of 5 to 10 times the salinity of the Salton Sea (California Department of Water Resources, 1970; Shinn, 1976) would be expected to eliminate pileworms from the affected area, as well as other benthic and pelagic organisms. These adverse effects could be caused not only by the excessively high salinity *per se*, but also by concomitant elevated temperatures or reduced oxygen concentrations. Pileworm larvae are in the Salton Sea plankton all year (Carpelan and Linsley, 1961a, b), and so there would be a constantly available source for recolonization. Only if there were contamination by heavy metals would there be a long-term problem (Reish and Carr, 1978). Thus, it is unlikely that a spill of even highly saline geothermal waste brines would have any more than a temporary and localized effect on the population of *N. succinea* in the Salton Sea.

The present experiments indicate that reproduction of *N. succinea* in the Salton Sea will continue with undiminished success at salinities at least as high as 45‰, and probably as high as 50‰. This means that gradually increasing salinities of the Salton Sea will not adversely affect the pileworm until some years after the collapse of the sportfishery, which seems sensitive to salinities no higher than 40‰.

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SUMMARY

The polychaete annelid *Nereis* (*Neanthes*) *succinea* is the major benthic detritivore in the Salton Sea, an inland salt lake in southeastern California, and is critical in the trophic chain leading to the sportfishery. In view of the increasing salinity of the Salton Sea, laboratory experiments were conducted to determine critical upper salinity limits for reproduction and survival of pileworms. Atokous (immature) pileworms can survive for extended periods in Salton Sea salinities at least as high as 65‰, with some reduction of survival in 70‰, and with only short term survival in 80‰, more than twice the present salinity of the Salton Sea (36‰). Heteronereid production is depressed by salinities higher than 50‰. Reproduction of *N. succinea* is successful at salinities at least as high as 45‰, and probably as high as 50‰. Fertilization and early cleavage stages are less tolerant of elevated salinities than are later development stages such as trochophores.

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